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► To cite this version:

Christophe Godin, Pascal Ferraro. Self-similar Analysis of Plant Architecture Reveals Hierarchical Classes of Meristem States. 5th International Workshop on Functional Structural Plant Models, Nov 2007, Napier, New Zealand. pp.481-484. hal-00306626

HAL Id: hal-00306626

<https://hal.science/hal-00306626>

Submitted on 9 Dec 2008

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Self-similar analysis of plant architecture reveals hierarchical classes of meristem states

Christophe Godin¹, Pascal Ferraro²

¹ INRIA Sophia-Anitpolis, Equipe Virtual Plants, UMR Dveloppement et Amlioration des Plantes, TA40/02, 34398 Montpellier Cedex 5, France

² LABRI, Universit de Bordeaux I

Keywords : Self-similarity ; meristem ; tree reduction; inverse problem;

Introduction

Apical meristems are small embryogenic regions, located at the tip of plant axes, that build up plant organs by cellular division. The production of the meristems depends on their internal physical, physiological and genetic state and is controlled by contextual factors (like micro-environment, availability of nutrients, *etc.*). In principle, the number of variables that may be used to define the state of a meristem, taking account the nature and the concentrations of molecules in each cell, their position, the physical stresses at each point, the geometry of cells, their genetic contents, *etc.*, is infinitely large. Due to this intrinsic complexity, and to the current lack of hindsight on processes at such small scales, the connection between a meristem state, its micro-environment and what it produces at varying time scales seems until now largely out of reach.

However, the remarkable organization of plants at macroscopic scales makes the situation not so hopeless. The fact that plants are made up of the repetition of many similar components, at different scales e.g. [?, ?, ?, ?, ?, ?], provides macroscopic evidence for regularities and similarities in processes that drive meristem activity at microscopic scales.

In this paper, we propose to formalize this connection between macroscopic observations and microscopic, mostly invisible, processes. To achieve this connection, we formulate the following simplifying, though fundamental, scaling hypothesis :

Scaling hypothesis: *If two branching structures in a plant are similar, they were probably produced by meristems with similar state and context.*

In this presentation, we shall show that it is possible to use this idealized - but useful - hypothesis to organize the multitude of meristem states and contexts by classes of equivalence with respect to the similarity of what they produce.

In this first approach, the similarity between branching systems is considered to be purely structural (no geometry is taken into account for instance). Due to the nested nature of these structures, we show that the study of similarities between all parts of a plant boils down to studying the self-similar nature of the plant structure. Based on previous attempts to quantify self-similarity in plants [?, ?], we introduce a new method that enables us to define the degree of self-similarity of any plant.

This definition relies on the construction of a directed acyclic graph (DAG) corresponding to the reduction of the initial tree, when all the structural redundancy has been removed. Under the scaling hypothesis, the nodes of this graph can be interpreted as meristem states, and the edge between two states would denote the occurrence of a meristem differentiation (from the source to

the target state). Paths in the graph therefore denote all possible meristem differentiation sequences. If this DAG is linear (i.e. can be represented by a chain), the plant is said *self-similar*. In self-similar plants, there is thus a unique differentiation sequence for all the meristems of the plant. We show that it is possible to compute, for any given plant, the smallest self-similar plant which contains it. This makes it possible to define a unique differentiation sequence of meristem states for any plant and to associate each branching system of the original plant with one of these computed, hypothetical, meristem states.

The hierarchical organization of the meristem computed in this way could be used as a guiding canvas to analyse the microscopic nature of meristems.

From biology to mathematical formalization: modelling plant architecture self-similarity

Definition of an equivalence relation on branching systems. Different strategies can be used to define an equivalence relationship between branching systems. They can be equivalent because they have the same root diameter, because they have the same size or because they bear the same number of flowers. Here we consider structural equivalence. Formally, this comes down to defining a notion of isomorphism between branching systems. In [?], we defined isomorphism between axial branching systems (i.e. branching systems for which a trunk is defined). Here we consider a less restrictive class of isomorphism between branching systems which holds for any type of tree structure.

Definition 1 (tree isomorphism) Let $T_1 = (V_1, E_1)$ and $T_2 = (V_2, E_2)$ be two rooted trees. A bijection ϕ from V_1 to V_2 is a tree isomorphism if for each $(x, y) \in E_1$, $(\phi(x), \phi(y)) \in E_2$.

To compute whether two branching structures T_1 and T_2 are isomorphic, we use a notion of edit-distance between trees [?, ?]. This distance is defined as the minimal number of elementary edit operations (insert, delete or match vertices) that is necessary to transform T_1 into T_2 : $D(T_1, T_2) = \min_S \sum_{s_i \in S} s_i$. This distance has the following property:

Property 1 $D(T_1, T_2) = 0 \Leftrightarrow T_1 \equiv T_2$

Definition 2 (Reduction of a tree) Let T be a tree, we denote by $\mathcal{R}(T)$ the graph obtained by quotienting T by the equivalence relation \equiv .

It can be shown that this graph is a DAG and that there exists an algorithm that can compute this DAG in time $O(|T|^2 \ln |T|)$ [?]. A DAG for which there exists a path going through all its vertices is said *linear*.

Definition 3 (Self-Similar tree) A tree T is self-similar if $\mathcal{R}(T)$ is linear.

Among all the self-similar trees, we consider those trees that contain T , denoted as $\mathcal{S}(T)$. Then, we consider trees T^* in this set that minimize the distance with T .

Definition 4 (Smallest Self-similar Tree, SST) *Let T be a tree and $\mathcal{S}(T)$ be the set of all the self-similar trees that contain T . Then, we define the set of smallest self-similar trees containing T by: $SST(T) = \{T^* | T^* = \underset{T' \in \mathcal{S}(T)}{\operatorname{argmin}} D(T, T')\}$*

We show that, for any tree T , it is possible to compute an element $T^* \in SST(T)$ in polynomial time $O()$, and give the corresponding algorithm.

Example: hierarchical organization of meristem states in Rice

The above approach was tested on different plant architectures. We present here results corresponding to the analysis of a rice panicle, already described in [?], Fig. 1. The topological structure of the panicle, T , is depicted in Fig 2.

Figures ...

We first compute the reduction tree $\mathcal{S}(T)$, Fig. 3. This graph, from which the original tree can be reconstructed [?], is not linear and show a number of different meristem differentiation sequences. By computing an element T^* of $SST(T)$ (Fig. 4), it is possible to find a single sequence of meristem state differentiation. The states of this sequence can be subsequently projected on the original topological structure, thus providing an interpretation of the entire structure in terms of meristem differentiation (Fig. 5)

Perspectives: from mathematical formalism back to biology

Due to the new technological and scientific progresses in molecular biology, imaging and developmental biology, the possibility to open up the meristem blackbox enables us to start seeking for processes and variables that determine at first order a meristem state and the nature of its growth context.